On Some Points in the Kinetogenesis of the Limbs of Vertebrates.

By E. D. Cope.

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The following paper is designed to supplement some omissions from my previous discussion of this subject in the memoir "On the Mechanical Causes of the Origin of the Hard Parts of the Mammalia."*

I. The Segmentation of the Chiropterygium.

The segmentation of the limbs in the Vertebrata is a simple mechanical problem. Paleontology and embryology concur in proving that the limbs originated in primitive folds in the external integument, and that their connection with the internal skeleton was of later accomplishment. At first free, they sought points of support on the skeleton, but did not lose their free mobility when this contact was attained. Appropriately to the mechanical conditions of rigidity and flexibility necessary to their use in a fluid medium, they were originally composed of slender rods which were segmented by interruptions at suitable points. The articulations of the fin rays of fishes have been made the subject of an interesting research by Ryder, who finds them to be fractures, due to flexures during motion in the water medium.† The limb of land vertebrates (the chiropterygium) was derived from one of the forms of fins (rhipidopterygium) of water vertebrates. This is the simple type of primitive fin displayed by the Paleozoic Teleostomi of the superorder Rhipidopterygia. Whether the subdivisions of the chiropterygium, the propodial, metapodial and phalangeal bones, etc., were divided from the primitive branches of the archipterygium, as held by Gegenbaur; or whether they have developed by sprouting from a simple axial series of segments, as held by Baur ; or whether, as I have suggested, it is a derivation from the rhipidopterygian type of paired fin (Fig. 1, p. 280), is not yet decided. In either case, the limbs of the first land animals were segmented and flexible at the joints between the segments. The necessities of such limbs are twofold : first, to serve as supports when at rest or in progression ; second, to be applied to the body in protection from enemies, or in aiding the functions of feeding, reproduction, etc. The first function requires principally mobility at the point of connection with the body. The second, flexibility at some point on the shaft of the limb. The two kinds of movements in question would conserve two principal points of flexure, and these would be for the fore limb, just what we find, the shoulder and elbow joints ; and for the hind limbs, the hip and knee joints. The two median joints are directed in opposite ways, the elbow backwards and

* American Journal of Morphology, iii, 1889, p. 137.

† Proceedings of the American Philosophical Society, 1889, p. 547.

the knee forwards. This diversity is clearly due to the diverse positions of the functioning regions. The opposite extremities of the alimentary canal, the posterior including the exits of the urogenital organs, requires that the fore limbs should bend forwards, and the posterior limbs backwards. And the constantly recurring necessity for the exercise of these flexures must necessarily have developed the appropriate articulations in preference to all others. The terminal flexure, that of the wrist or ankle, has been evidently due to a similar mechanical cause; viz., the flexure due to pressure of the weight of the body on the terminal segments when in contact with earth. The distal segments are the most slender in all types, and least able to maintain a linear direction under pressure, hence, they have flexed easily and thus the line of separation between leg and foot had its origin.

II. The Origin of the Crests of the Humeral Condyles.

I have already pointed out (*op. cit.*) the kinetogenetic origin of the tongue and groove articulations in the Mammalia.

An excellent example is furnished by the elbow joint of the Quadrumana and Diplarthra. In the lower Mammalia, including the Carnivora (*op. cit.*, Pl. ix, fig. A), the distal end of the humerus presents a submedian groove which receives the ulna, and on the inner side of it, a more or less convex surface, which is applied to the head of the radius. The coronoid process of the ulna is narrow and its dense bounding walls impinge on the broad face of the humeral condyle in flexion and extension, and transfers to it the force of impact when the foot strikes the ground. In either case, strong pressure has been brought to bear on the humeral condyle and it has yielded to the denser body of the ulna, thus forming the groove in question. In such Mammalia, the effect of the head of the radius on the humeral condyle has been similar and in the same direction, *i. e.*, upwards. The dense edges of the former have impressed themselves on the latter, while the unsupported middle portion has yielded in the direction of gravity, and the result is what we find, *i. e.*, a cup-shaped surface of the head of the radius, and a convexity of the humeral condyle, adapted to it.

Among specializations of the elbow joint, I call attention to two. In the Quadrumana, the head of the radius, probably owing to continued supination of the manus, occupies a position at the external side of the coronoid process of the ulna, and impinges on the outer part of the condyle of the humerus. The concavity of its head and the convexity of the humeral condyle are visible as before, but a prominent tongue or keel, which has been called the intertrochlear crest, separates the ulnar and radial surfaces of the humerus. (Fig. B). This keel occupies the groove or interval which separates the head of the radius from the coronoid process of the ulna. It is plain that we have here another tongue and groove joint, produced by the mutual adaptation of parts, under strain, pressure and impact. The other extreme of elbow joint is found in

that of the diplarthrous Ungulata (Fig. E). Here the head of the radius, while retaining its normal position on the inner side of the forearm, is extended to the external side of the ulna and even beyond it, adapting itself to the entire width of the humeral condyles. The same structure is found in the specialized forms of both series of Diplarthra, the Perissodactyla and Artiodactyla. This expansion of the head of the radius appears to be in direct relation to the duration through long geologic ages of the impacts which have affected the limbs of these, the swiftest of the Mammalia. That the head of the radius should be spread so as to fit the entire surface of the humerus as an effect of continued impact, seems to be a mechanical necessity. But in addition to this we find a tongue-and-groove adaptation in which the crest (which I have called the trochlear crest), articulates with a groove in the head of the radius. The internal articulation of the humerus with the radius has the usual form, convex and concave distad. The trochlear crest marks the external border of the olecranar groove of the humerus. But the external part of the humeral condyles is converted into a roller which is set off from the trochlear crest, by the abrupt contraction of its diameter ; while the corresponding part of the head of the radius projects to fit it exactly.

A probable explanation of the form of this roller may be derived from a consideration of the almost identical structure of the metapodio-phalangeal articulation in the Artiodactyla. The internal and external sides of the distal metapodial condyles are not similar ; a character very distinct in the Artiodactyla (Fig. E). This is simply due to the unequal pressure exerted on the two extremities of the condyle by the phalanges, owing to the divergent direction of the digits when serving as a support. In the distal end of the humerus, the same effect is seen, the external part of the condyle nearly resembling the corresponding part of the meta podial bones. This is traceable to the same cause, viz., the divergent position assumed by the forearm on the humerus, when the weight is sup ported on one fore leg only. This brings the line of pressure through the external part of both the head of the radius and the humeral condyle (Fig. 42).

Although I have already given what is essentially the same explanation of this structure (*op. cit.*, p. 199), the above renders clearer some points

III. Atrophy of the Ulna and Fibula.

Successive atrophy of the ulna and fibula is coextensive with reduction of the number of the digits in the ungulate Mammalia, and with the development of the digital patagium in the bats. This is in broad contrast to the subequal development of the ulna and radius in the Cetacea, where the fore limb functions as the blade of an oar. The cause of the reduction of the two elements in the Ungulata is the restriction of the functions of the fore and hind limbs to the radius and tibia respectively. The distal extremities of the ulna and fibula in primitive Ungulata were sup-

ported by the external bones of the carpal and tarsal series respectively. The reduction of the external digit deprives the external bones in question of their share in the support of the general weight, and consequently relieves them of impact, which now passes through the longer median digits which remain. The median digits, on the other hand, support the radius and tibia through the medium of the carpus and tarsus, and it is these elements, therefore, which function in the use of the limb. We have here an evident illustration of the effect of disuse in effecting the atrophy of an element, and of use in increasing the size and complexity of an adjacent element of the same organism. No other explanation seems possible, for the elements which are reduced and those which are enlarged are subjected in every other respect to the same conditions.

On False Elbow Joints.

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I have in various papers formulated and defended the hypothesis that the peculiar characters of the articulations of the mammalian skeleton are due to mechanical causes operating throughout the ages of geologic time.* I had previously traced the succession of these modifications from simple reptilian types, through various stages, to the highly specialized and mechanically perfect structures seen in the higher Mammalia. The series of forms revealed by paleontologic research is so complete as to leave little doubt in the mind as to the manner and cause of their origin. The theory thus derived, which I have called kinetogenesis, depends for its demonstration on two assumptions. The first is that living osseous tissue is plastic, and is therefore readily modified in its form by impacts, strains, friction, etc. ; and the other is that one which is necessary to all evolutionary hypotheses, that acquired characters are inherited. I do not propose to discuss here the latter proposition, but I desire to offer some evidence in support of the former. Marey tells us,† as a result of a study of pathological conditions of articulations, that "after dislocations the old articular cavities will be filled up and disappear, while at the new point where the head of the bone is actually placed, a fresh articulation is formed, to which nothing will be wanting in the course of a few months ; neither articular cartilages, synovial fluid, nor the ligaments which retain the bone in place."

Specimens demonstrating the truth of this statement of Marey are also

* *Origin of the Fittest*, 1887, p 368 *et seq.*; "The Mechanical Origin of the Hard Parts of the Mammalia," *American Journal of Morphology*, 1889, p. 148.

† *Animal Mechanism*, 1874, pp. 88, 89.